REPRODUCTIVE AND MATERNAL BEHAVIOR OF THE MANTIS SHRIMP *GONODACTYLUS BREDINI* MANNING (CRUSTACEA : STOMATOPODA)

HUGH DINGLE AND ROY L. CALDWELL

Department of Zoology, University of Iowa, Iowa City and Department of Zoology, University of California, Berkeley

The mantis shrimp *Gonodactylus bredini* is an active predatory marine crustacean distributed in tropical and sub-tropical waters of the Western Atlantic (Manning, 1969). It lives in cavities in rocks and rubble in littoral and sub-littoral zones and defends these cavities vigorously. This defense involves elaborate behavior patterns including spreading of the raptorial meri in a posture which appears to serve as threat and use of the raptoral appendages to strike an opponent. Details of this aggressive behavior have been analyzed utilizing extensive records from homosexual interactions (Dingle, 1969a; Dingle and Caldwell, 1969). This behavior is apparently characteristic of the family Gonodactylidae since it occurs also in *G. oerstedi* (Caldwell, unpublished), *G. spinulosus* (Dingle, 1971), *Haptosquilla* (*Gonodactylus*) *glyptocercus* (Serène, 1954) and in several Pacific and Indian Ocean species (Caldwell and Dingle, unpublished).

Species of *Gonodactylus,* along with those from other genera and families of stomatopod, also exhibit an elaborate maternal behavior (Giesbrecht, 1910; Verrill, 1923; Serène, 1954). The female lays her eggs in a compact mass which she constantly kneads with her maxillipeds; she remains with eggs and newly hatched larvae until the latter mature to the planktonic stage and leave the burrow or cavity (Dingle, 1969b). The only description of stomatopod courtship in the literature is that of Serène (1954) who describes it for *Haptosquilla glyptocercus.*

The initiation of courtship behavior in *Gonodactylus* must involve highly specific communication between potential mates to insure that pre-copulatory rather than aggressive interactions take place. Indeed in many heterosexual encounters the interaction is an aggressive one (Dingle and Caldwell, 1969). There must therefore be some exchange of signals leading to courtship rather than to aggression. Elaborate signaling during courtship is of course well-known in semi-terrestrial crabs (Crane, 1966; Salmon and Atsaides, 1968; Schöne, 1968; Wright, 1968), shrimp (Johnson, 1969), and various hermit crabs (Hazlett, 1966, 1968). In view of the widespread interest in crustacean behavior and communication and the complexity of behavior in *G. bredini,* a study of reproduction in this species seemed of interest.

MATERIALS AND METHODS

The species *Gonodactylus bredini* has previously been described as *G. oerstedi* (Verrill, 1923; Hazlett and Winn, 1962; Dingle, 1964), but the two species are now recognized as distinct (Manning, 1969). *G. bredini* is the only one recorded

from Bermuda although the two are sympatric and occupy similar habitats throughout the West Indies.

This study was done at the Bermuda Biological Station, St. George's West, Bermuda. Most data were taken during June and July, 1968, with a few observations from the same months in 1966.

The animals were obtained by breaking up pieces of rock collected in shallow water at low tide. They were returned to the laboratory and maintained in sea water either constantly running or changed daily. Some animals were supplied with chambered rocks similar to those they occupied in nature, but most were induced to occupy 50 or 100 ml Erlenmeyer flasks. These flasks were wrapped in black polyethylene in which a flap was cut to permit observation of the interior without disturbing the animal. All animals were fed daily with pieces of various fish and crustaceans. Each individual or pair was housed in its own container; this is necessary because of the aggressive nature of these animals.

All courtship and copulation sequences were observed in an open flat-bottomed bowl, 19 cm in diameter, with a sand covered bottom. Observations on maternal behavior were made on females housed in polyethylene covered Erlenmeyer flasks.

<center>RESULTS</center>

Courtship and copulation

A courtship sequence leading to copulation is initiated when either the male or the female approaches the other individual. If the male approaches first he spreads the raptorial meri two or three times and then may swim over the female; he then usually palpates her body with his antennules although not uncommonly this is omitted. With or without antennular palpation, the male then grasps the female with his maxillipeds most often at the telson. He then works his way up her body until he is holding her by the carapace with maxillipeds 4 and 5 using the hooked dactyls to grasp the rim. While he is holding her he strokes her carapace with the small first maxillipeds and with the third maxillipeds which are similar to 4 and 5 (the 2nd maxillipeds are the raptorial appendages and are not used during clasping). All the while the female remains virtually motionless. If the female makes the initial approach, she does so from the front or side of the male, not from the rear. When she reaches him, she pushes her head and carapace beneath his cephalothorax which usually induces him to grasp her carapace as indicated above. While still grasping the female's carapace, the male curls his abdomen forward while the female turns half over on her back (Fig. 1); he then brings his gonopods up to oppose her genital openings which are paired submedian structures ventrally located on the sixth thoracic segment. The male gonopods are a pair of tubular structures located at the bases of the last pair of walking legs on the last (eighth) thoracic segment. For the next 10 to 50 seconds the pair remains thus with the male firmly clasping the female's carapace behind the eyes and making thrusting movements with his abdomen while the female is completely relaxed. At the completion of copulation, either the male releases and swims slowly away while the female turns back over on to her ventral surface or the female pushes the male off with her telson and struggles free. Immediately after separation the male may strike the female gently with the raptorial appendages; this post-copulatory strike resembles the aggressive strike in form, but is delivered at

much slower speed and with very little force.   A tap would be a good description for it.

The courtship-copulation sequence takes place only if the female is receptive. If she is unreceptive, she attacks all other individuals, male or female, which are placed with her.   In most cases, it is the female which determines subsequent behavior after initial contact; in 20 out of 22 heterosexual aggressive interactions the female attacked first.   This attack consisted of a rapid approach to the male
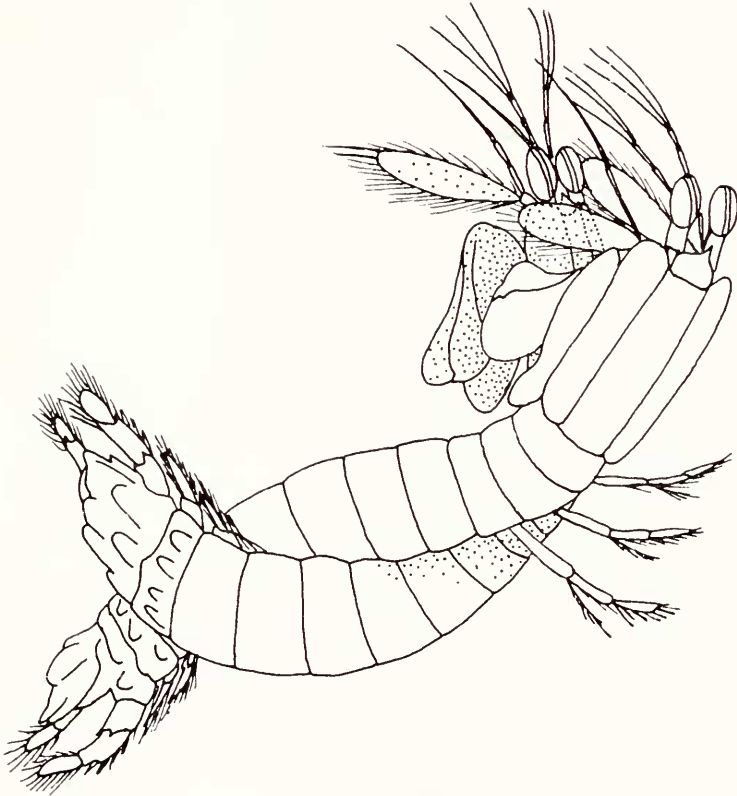

FIGURE 1.   Mating in *Gonodactylus bredini* with male above clasping carapace of female below (stippled).

followed by a strike delivered with the raptorial appendages (for detailed description see Dingle and Caldwell, 1969).   The attack and strike in all but one case took place within the first 15 seconds after the animals were paired; the one exception took approximately 30 seconds.   Receptive females were reluctant to attack as indicated by three encounters between pairs of receptive females.   Eventually these pairs fought, but only after an interval of 1–3 minutes.   The interval before two males began fighting varied from a few seconds to about one minute.

A receptive female can generally be distinguished by the appearance of the ovary and hepatopancreas complex.   These organs run the length of the abdomen

dorsal to the digestive tube and project into the telson (Balss, 1938). The portions in the telson are visible through the ventral surface. In non-receptive females the visible portions are light in color and have a dendritic appearance. In the receptive female the portions in the telson are extremely dark and are considerably swollen; it has not yet been possible to determine if ovary, hepatopancreas, or both are responsible for the darkened telson, although morphological comparisons following dissection suggest that changes occur in both (M. Reaka, University of
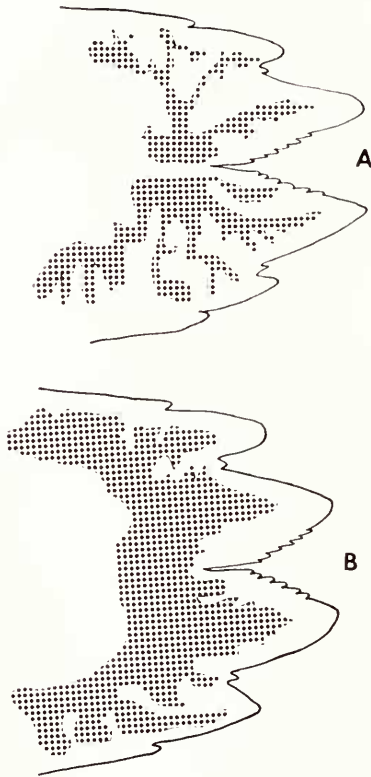

FIGURE 2. Ventral view of telson of (A) non-receptive female and (B) receptive female.

California, personal communication). The externally visible difference is illustrated in Figure 2. In 11 out of 12 cases where the ovary-hepatopancreas complex was dark and swollen, copulation took place shortly after the initial encounter with a male. In the other case the female attacked, but the male was behaving abnormally and in fact died the next day. In one case a female copulated when there was no obvious darkening and swelling. In this case, however, the complex had an unusual mottled appearance which was by no means that normal for an unreceptive female. Female receptivity was not connected with the molt as it is in many other crustaceans (Schöne, 1961; Hazlett, 1966).

Male receptivity to courtship and copulation is more difficult to determine, and there seem to be no morphological criteria to distinguish receptive males. Most

males, however, seem ready to copulate almost continuously except immediately following a previous copulation at least during the period of our observations (June and July). Although a female would copulate with another male within 5 minutes after a pairing, males for the first few minutes showed no interest in a second receptive female even though she would approach and push under the male's cephalothorax. Most males would copulate again after approximately 20 minutes, but two males still showed no interest in receptive females 24 hours after a copulation. In one instance (out of 12 trials) a male showed no interest in a receptive female even though he had no previous contact with a female of any sort for a week. This was not a function of the female, for she copulated immediately with a second male. The reasons for the first male's behavior are unclear; it did not seem to be connected with a pre-molt period. This male did copulate several days later.

In an effort to determine if males would attempt to copulate with non-receptive females which were prevented from attacking, six such females were anesthetized in a solution of 2% ether in sea water and males placed with them. In two cases the males completed the whole courtship sequence except copulation itself; this failure to copulate was apparently because the males were unable to turn the females over and were thus unable to bring their gonopods up to the female's genital opening. In a third instance the male undertook the initial stages of courtship up to palpation of the female's body with the antennules, but then broke off the encounter and paid no further attention to the female. In the remaining cases, there was no obvious courtship behavior although some contacts involved antennular palpation which may have been incipient sexual activity.

Egg-laying and maternal behavior

Following copulation the male and female share a chamber until the eggs are laid. Further copulations may take place during this period. The interval between first copulation and egg-laying was about 10 days at a water temperature of 24–26°. This is the only time when 2 animals share a cavity as indicated by data from both field and laboratory. For example, in the field we collected about 200 animals in the two summers of 1966 and 1968 and found only 4 cavities occupied by 2 animals. In all 4 cases they were male and female, and the ovary-hepatopancreas complex of the female was dark and swollen; also in all 4 cases the female laid eggs shortly after capture. In the laboratory, the male and female jointly occupy a chamber when provided with one and do not engage in aggressive interactions with each other. Both, however, defend the chamber against other stomatopods of both sexes in the period before the eggs are laid. Within 24 hours after laying, the female evicts the male and prevents his return by the appropriate aggressive behavior. Under laboratory conditions, the male may be able to re-occupy the chamber since in the aquaria where the animals were housed, there was usually no other cavity available. The female's aggressiveness increases, however, until the male is no longer able to re-occupy unless he is conspicuously larger than she is in which case he may evict her. In the field evicted males evidently do not return to the chamber since a male was never found in a chamber with a female attending eggs or young. The course of post-laying aggression in one female is

indicated in Figure 3; this female was captured with a male but was kept alone with her eggs after laying and males were introduced at intervals. The increase in aggressive behavior is obvious.

Once the eggs are laid and the male evicted, the female remains in the chamber with the eggs and after hatching with the larvae. She frequently palpates the egg mass or holds it with her maxillipeds slowly turning it over. This behavior ap-
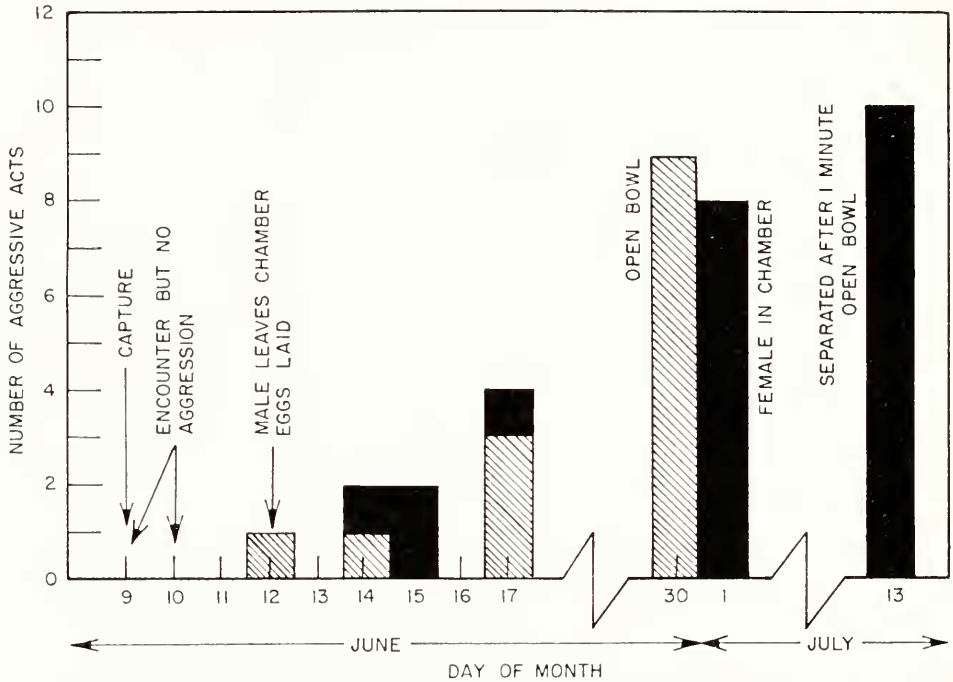

FIGURE 3. Increase in aggressive tendency of a female following egg-laying. Interactions were observed between this female and the male captured in the cavity with her, except for July 1 when a strange male was introduced. Hatched bars indicate number of aggressive acts directed toward a male that did not involve a strike; solid bars indicate strikes. "Open bowl" indicates interactions when the female was removed from her cavity and placed with a male; "female in chamber" indicates interactions when the female was in her "home" cavity, and a male was introduced into the bowl containing the cavity. Brief open bowl encounters were observed on June 9 and 10 when both animals were outside the chamber. On June 12 eggs were laid, and the male left the chamber and was removed to another bowl.

parently serves to keep the eggs clean since several isolated masses became contaminated with what are evidently ciliates (R. Kinzie, University of Hawaii, personal communication) and some algae. When defending the cavity, the female leaves the eggs in the recesses of the chamber and comes to the entrance. During this defense she may coil and back into the eggs; this has led to the erroneous statement, originated by Brooks (1886), that the females carry the egg mass over the back (cf. Barnes, 1968). The larvae when they hatch are photonegative and attach themselves to any surface they encounter and thus are behaviorally adapted

to remaining in the chamber (Dingle, 1969b). The female remains with them until the molt to Stage IV at which point they become strongly photopositive and leave the chamber to enter the plankton. The first 4 larval stages are described by Manning and Provenzano (1963). The period from the time the eggs are laid until the time the larvae enter the plankton is approximately 30–35 days at 24–26° C. On two occasions females with eggs were noted outside the chamber, but returned to it immediately when approached. The egg mass was left in the chamber during an excursion.

Both males and non-receptive females will carry an egg mass if presented with it, but usually drop it after a short period or begin to eat the eggs. They are especially likely to eat the eggs if they become separated from the matrix that maintains the cohesiveness of the egg mass. Males seem particularly inclined to eat eggs, and this is probably a contributing factor to the eviction of the male following egg-laying.

Discussion

When both male and female specimens of *Gonodactylus bredini* are receptive, mating takes place rapidly and the associated behavior is relatively simple and straightforward. The entire sequence from first encounter to release of the female following copulation can take place in between one and two minutes. Reproductive behavior in stomatopods contrasts with the highly complex mating behavior and pair formation observed in many other Crustacea (Schöne, 1961, 1968; Hazlett, 1966, 1968; Johnson, 1969; Atema and Engstrom, 1971) and resembles the situation described, for example, in the spider crab, *Libinia emarginata* (Hinsch, 1968). Also of interest is the fact that there is no aggressive behavior prior to mating even though aggressive behavior in non-sexual situations is very marked in *G. bredini*. Indeed non-receptive females attack males almost immediately.

The absence of aggressive displays during sexual encounters implies that there are precise signals allowing for rapid recognition. In females readiness to mate may be signaled by failure to attack. This is suggested by two results. First, when males were placed with non-receptive females, it was invariably the females which attacked first. Secondly, on 3 of 6 occasions, males displayed sexual behavior toward anesthetized females which had previously been shown to be non-receptive (*i.e.*, they did not possess dark telsons (Fig. 2), and they attacked males). In this *G. bredini* resembles some gammarids and decapods, where any individual which does not resist is seized and treated as a female (Schöne, 1961). The signals from a female which initiates mating are obvious since she approaches and forces her head under the male's carapace; in the same situation an aggressive female approaches far more rapidly, usually with the raptorial meri widely extended laterally, and invariably strikes. A role for the female as the initiator of sexual behavior is somewhat unusual, but not unknown among Crustacea (Schöne, 1961). Limited observations suggest that such a role is even more marked in another gonodactylid, *Pseudosquilla ciliata* (Caldwell and Dingle, unpublished observations).

Whatever else may determine receptivity in *G. bredini*, the molt is evidently not involved. In this, *G. bredini* is like several other Crustacea representing diverse groups, *e.g.*, xanthid crabs (Knudsen, 1960), hermit crabs (Hazlett, 1968),

and majid crabs (Hinsch, 1968). It seems evident that mating systems independent of molting are by no means uncommon in crustaceans and may in fact occur as frequently as the molt-associated systems once thought to be the predominant mode (Schöne, 1961). In *G. bredini* a receptive female, while not soft from a molt, is still distinguishable morphologically because of the dark telson.

The absence of molt-associated mating raises the question of pheromones since these substances have long been thought to be associated with molting individuals and have recently been demonstrated in mating (Ryan, 1966; Atema and Engstrom, 1971). We have not demonstrated a pheromone in *G. bredini* courtship nor have we seen any evidence to suggest one. This, of course, does not mean one is not present although we think it unlikely. Mating takes place so rapidly and the non-pheromonal signals seem so clear, *e.g.*, a receptive female does not immediately attack, that a pheromone seems unnecessary for successful mating.

Finally, the relatively simple mating behavior but relatively complex prespawning and maternal behavior of *G. bredini* would seem to be adaptations to cavity living. Burrow or cavity living with associated defensive behavior would afford protection to developing eggs and young. It would not, however, favor elaborate courtship involving visual displays, fencing, circling, etc. (*e.g.*, Hazlett, 1966; Johnson, 1969; Atema and Engstrom, 1971); this is because the cavity is dark, thus limiting vision, and constrained, thus limiting movement. The only visual element in the sexual behavior of *G. bredini* is the approach (usually by the male) with some spreading of the meri; in nature this undoubtedly takes place at the cavity entrance. A female can identify an entering stranger and a male can identify a receptive female in the same way: an appropriate partner approaches slowly or accepts an advance while an inappropriate one attacks. The remaining behavior seems to involve predominantly tactile inputs and is performed with an economy of movements as the male works his way up the back of the female and finally copulates with her. The joint occupation of a cavity by a male and female prior to spawning probably evolved for two reasons: it is advantageous for the male to insure that he alone fertilizes a given egg mass, and for the female because it provides for additional defense during the spawning period. In sum the reproductive behavior of *G. bredini* seems to reflect the co-evolution of four elements: cavity dwelling, defense of the cavity, courtship and copulation, and maternal care. The same is undoubtedly true for *Haptosquilla glyptocercus* and other Gonodactylidae because both Serène's (1954) observations and our own (unpublished) indicate that the behavioral repertoire of these species is very similar to that of *G. bredini*.

SUMMARY

1. Courtship and copulation are brief in *G. bredini*. Either sex can indicate courtship by approaching; after antennular palpation the male then grasps the female by the carapace and copulation takes place.

2. Receptive females can be distinguished morphologically by darkened internal organs visible through the telson and behaviorally by their acceptance of a male's approach. Unreceptive females attack males immediately.

3. Males share cavities with females during the few days prior to spawning. Following egg-laying females defend cavities against males. The eggs are kept in the cavity and frequently manipulated; the newly hatched larvae remain in the cavity with the female until they reach Stage IV.

4. The form and duration of reproductive and maternal behavior in *G. bredini* are apparently a consequence of cavity living.

LITERATURE CITED

Atema, J., and D. G. Engstrom, 1971. Sex pheromone in the lobster, *Homarus americanus*. *Nature*, 232: 261–263.

Balss, H., 1938. Stomatopoda. *Bronn's Klassen und Ordungen des Tierreichs*, 5: 1–173.

Barnes, R. D., 1968. *Invertebrate Zoology*. [2nd ed.] Saunders, Philadelphia, 743 pp.

Brooks, W. K., 1886. Report on the Stomatopoda collected by H.M.S. *Challenger* during the years 1873–76. *Rep. Sci. Res. Challenger, Zool.*, 16: 1–116.

Crane, J., 1966. Combat, display and ritualization in fiddler crabs (Ocypodidae, Genus *Uca*). *Phil. Trans. Roy. Soc. London*, 251: 459–472.

Dingle, H., 1964. A colour polymorphism in *Gonodactylus oerstedi* Hansen, 1895 (Stomatopoda). *Crustaceana*, 7: 236–240.

Dingle, H., 1969a. A statistical and information analysis of aggressive communication in the mantis shrimp *Gonodactylus bredini* Manning (Crustacea: Stomatopoda). *Anim. Behav.*, 17: 561–575.

Dingle, H., 1969b. Ontogenetic changes in phototaxis and thigmokinesis in stomatopod larvae. *Crustaceana*, 16: 108–110.

Dingle, H., 1971. Aggressive behavior in stomatopods and the use of information theory in the analysis of animal communication. Pages 126–156 in H. E. Winn and B. Olla, Eds., *Behavior of Marine Organisms—Recent Advances*. Plenum Press, New York.

Dingle, H., and R. L. Caldwell, 1969. The aggressive and territorial behaviour of the mantis shrimp *Gonodactylus bredini* Manning (Crustacea: Stomatopoda). *Behaviour*, 33: 115–136.

Giesbrecht, W., 1910. Stomatopoden. *Fauna e Flora del Golfo Napoli*, 33: 1–239.

Hazlett, B. A., 1966. Social behavior of the Paguridae and Diogenidae of Curacao. *Studies on the Fauna of Curacao and other Caribbean Islands*, 23: 1–143.

Hazlett, B. A., 1968. The sexual behavior of some European hermit crabs (Anomura: Paguridae). *Pubbl. Staz. Zool. Napoli*, 36: 238–252.

Hazlett, B. A., and H. E. Winn, 1962. Sound production and associated behavior of Bermuda crustaceans (*Panulirus, Gonodactylus, Alpheus*, and *Synalpheus*). *Crustaceana*, 4: 25–38.

Hinsch, G. W., 1968. Reproductive behavior in the spider crab, *Libinia emarginata* (L.). *Biol. Bull.*, 135: 273–278.

Johnson, V. R., 1969. Behavior associated with pair formation in the banded shrimp *Stenopus hispidus* (Olivier). *Pacific Sci.*, 23: 40–50.

Knudsen, J. W., 1960. Reproduction, life history, and larval ecology of the California Xanthidae, the pebble crabs. *Pacific Sci.*, 14: 3–17.

Manning, R. B., 1969. *Stomatopod Crustacea of the Western Atlantic*. University of Miami Press, Coral Gables, 380 pp.

Manning, R. B., and A. J. Provenzano, 1963. Studies on development of stomatopod Crustacea. I. Early larval stages of *Gonodactylus oerstedii* Hansen. *Bull. Mar. Sci. Gulf Carib.*, 13: 467–487.

Ryan, E. P., 1966. Pheromone: Evidence in a decapod crustacean. *Science*, 151: 340–341.

Salmon, M., and S. P. Atsaides, 1968. Visual and acoustic signaling during courtship by fiddler crabs (Genus *Uca*). *Amer. Zool.*, 8: 623–639.

SCHÖNE, H., 1961. Complex behavior. Pages 465–520 in T. H. Waterman, Ed. *The Physi-ology of Crustacea, Vol. II. Sense Organs, Integration, and Behavior.* Academic Press, New York.

SCHÖNE, H., 1968. Agonistic and sexual display in aquatic and semi-terrestrial brachyuran crabs. *Amer. Zool.,* **8**: 641–654.

SERÈNE, R., 1954. Observations biologiques sur les stomatopodes. *Ann. Inst. Oceanogr. Monaco,* **29**: 1–93.

VERRILL, A. E., 1923. Crustacea of Bermuda. *Trans. Conn. Acad. Arts Sci.,* **26**: 181–211.

WRIGHT, H. O., 1968. Visual displays in brachyuran crabs: Field and laboratory studies. *Amer. Zool.,* **8**: 655–665.